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Taxonomy and nomenclature of powdery mildew fungi: *Erysiphe asclepiadis*, *E. robiniicola* and *Golovinomyces caulicola*

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Abstract — The new species *Erysiphe asclepiadis* is described, illustrated and discussed. A new Chinese collection of *Erysiphe robiniicola* has recently been found that can be used to elucidate and discuss the confused taxonomy and nomenclature of this species and other taxa of *Erysiphe* s. lat. on *Robinia* spp. Based on a re-examination of type material in connection with the data given in the protologue, it can be shown that *Capnodium lygodesmiae* must be reduced to synonymy with *Ampelomyces quisqualis*. The confusion surrounding the name *C. lygodesmiae*, caused by the occurrence of the hyperparasite *A. quisqualis* on a powdery mildew fungus with abundant chasmothecia, is discussed in detail. The new combination, *Golovinomyces caulicola* (≡ *Spolverinia caulicola*), is proposed for the powdery mildew that serves as host of *C. lygodesmiae*.

Key words — *Erysiphaceae*, *Asclepias*, *Lygodesmia*

Introduction

The powdery mildews (*Erysiphales*) represent one of the most common groups of biotrophic fungi. They occur on a wide range of host plants including numerous ornamental and other important cultivated plants, and the distribution of many

of these fungi is cosmopolitan. Taxonomy and phylogeny of the *Erysiphales* in comparison with many other fungal groups is relatively well-known due to a monograph published by Braun (1987) and numerous phylogenetic examinations (Takamatsu et al. 1999, 2000; Hirata et al. 2000, Mori et al. 2000, Khodaparast et al. 2001, Braun et al. 2002, Matsuda & Takamatsu 2003, Hirose et al. 2005). Nevertheless, numerous taxonomic problems are still unresolved, various compound species (species complexes) are not yet treated in detail, and the knowledge on numerous powdery mildew diseases is insufficient since they are only known as anamorphic states. In the present paper, we try to reduce this knowledge gap. A new species is described, and the nomenclature and taxonomy of some older names is reassessed and discussed.

Materials and methods

The collections were mounted in distilled water and examined for description by means of standard light microscopy (Olympus BX 50, Hamburg, Germany) using oil immersion (bright field and phase contrast), but without any staining. Thirty measurements (× 1000 magnification) of conidia and other structures were made. The extremes are given in parentheses. The collections examined are deposited in the herbaria, BPI, HAL and NY (abbreviations according to Holmgren et al. 1990), and the Mycological Herbarium of the Tarim University, Xinjiang, China (HMTRM).

Taxonomy

1. A new species of the genus *Erysiphe* on *Asclepias tuberosa*

Erysiphe asclepiadis U. Braun & V. Kumm., **sp. nov.** FIG. 1

MycoBank, MB 512507

E. pachypodiae *similis, sed conidiis latioribus, 28–45 × 15–24 µm, ratione longitudinis/latitudinis (1.4–)1.5–2(–2.2), tubis germinalibus cum septis, appendicibus chasmotheciorum numerosis, brevioribus, apice non circinato.*

ETYMOLOGY: derived from the host genus.

MATERIAL EXAMINED: GERMANY. BRANDENBURG, Potsdam, Botanical Garden, on *Asclepias tuberosa* L. (*Apocynaceae* [*Asclepiadoideae*]), 7 Sep. 2004, V. Kummer *1457/Asclepias 1* (HAL 2273 F, holotype), holomorph; 15 Sep. 2008 (herb. V. Kummer *1457/Asclepias 2*), anamorph; 23 Sep. 2008 (HAL 2274 F), anamorph; 2 Oct. 2008 (herb. V. Kummer *1457/Asclepias 4*), holomorph.

MYCELIUM epiphyllous, in white patches or effuse, thin to moderately thick; hyphae branched, 3–8 µm wide, septate, hyaline, thin-walled, smooth to somewhat rough-walled. APPRESSORIA solitary or in opposite pairs, 3–8 µm diam., slightly to strongly lobed, occasionally nipple-shaped. CONIDIOPHORES arising from superficial hyphae, position between two septa non-central,

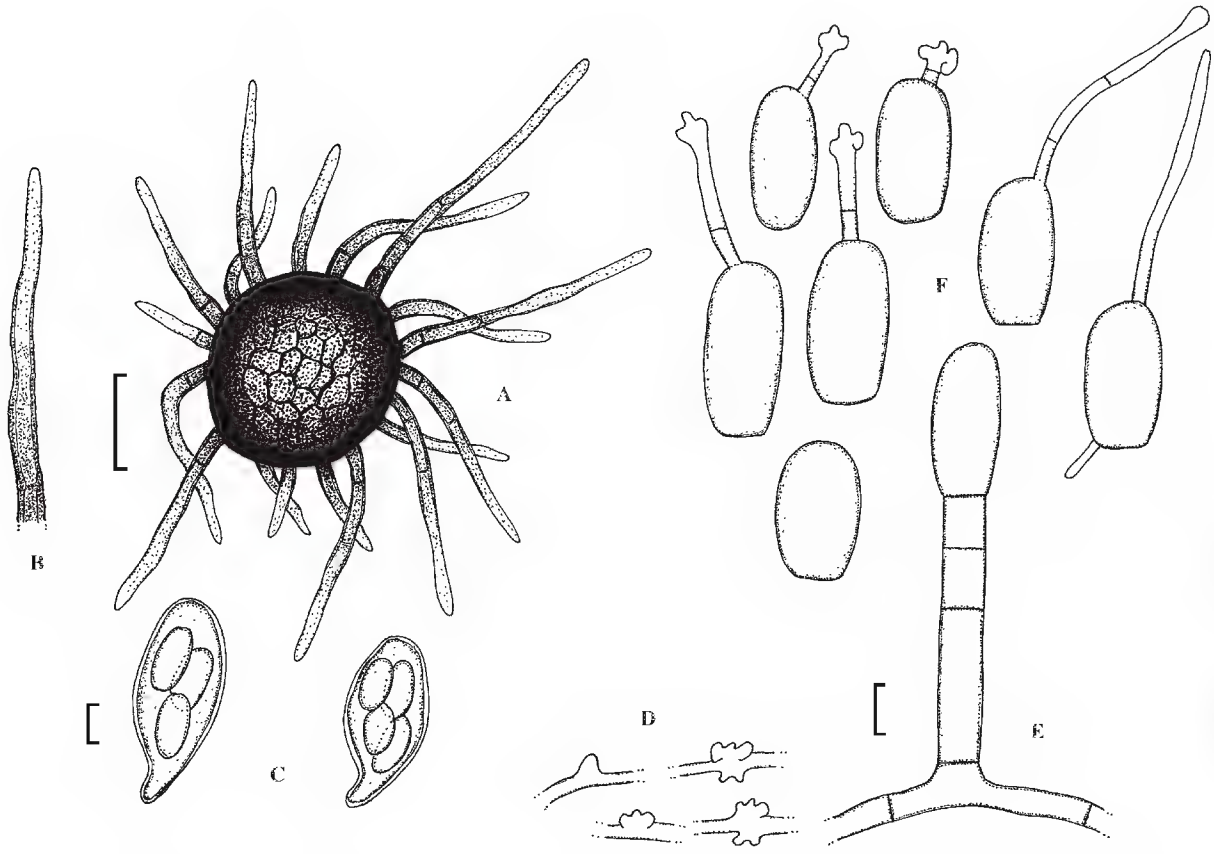

FIG. 1. *Erysiphe asclepiadis* (based on type material). **A.** Chasmothecium. **B.** Appendage. **C.** Asci. **D.** Appressoria. **E.** Conidiophore. **F.** Conidia with and without germ tubes. Scale bars = 50 µm (A, B), 10 µm (C–F). U. Braun del.

erect, straight, 40–90 µm long (without conidia), foot-cells 15–40 × 7–10 µm, cylindrical, straight, followed by 1–2(–3) shorter cells. CONIDIA formed singly, broadly ellipsoid(-ovoid), doliiform, 28–45 × 15–24 µm, length/width ratio (1.4–)1.5–2(–2.2), ends rounded to subtruncate, germ tubes terminal or subterminal, mostly short, with a terminal slightly to strongly lobed appressorium and a distinct septum in the lower half, some germ tubes (up to 25 %) long, up to six times as long as the conidial length, either without terminal appressorium and without septum or with a somewhat swollen, unlobed to slightly lobed appressorium and two septa, one septum in the lower and one in the upper half, i.e. the formation of septa in the germ tubes is initiated by the formation of terminal appressoria. CHASMOTHECIA scattered to gregarious, immersed in the mycelial felt, 75–115(–120) µm diam., subglobose; peridial cells irregularly polygonal, 10–25(–30) µm diam. APPENDAGES numerous, equatorial and in the lower half, 0.5–2 times as long as the chasmothecial diam. (up to 210 µm in length), (3–)4–10(–12) µm wide, somewhat narrower towards the apex, straight or almost so and stiff to flexuous, mycelioid, sinuous-subgeniculate, unbranched, (0–)1–3(–4)-septate, hyaline or brown

below and paler or colorless towards the apex, wall somewhat thickened below, up to 2 µm, thinner towards the apex, irregularly rough-walled. Asci 4–6 per chasmothecium, broadly obovoid to saccate, short-stalked, 50–70 × 30–45 µm, wall up to 3 µm thick, terminal oculus not very conspicuous, 10–20 µm diam., 3–5-spored, ascospores ellipsoid(-ovoid), colorless, (15–)20–26(–30) × 8–15 µm.

Comments: Lebeda et al. (2002, 2005) described *Erysiphe pachypodii* Lebeda et al. from the Czech Republic on potted plants of *Pachypodium lamerei* Drake cultivated in a private house. This is the only other species of the genus *Erysiphe* DC. described on a host belonging to the family *Apocynaceae* (including *Asclepiadaceae*). The size of the chasmothecia and the number and size of asci and ascospores agrees well with those of *E. asclepiadis*. However, *E. pachypodii* differs from the latter species in having a smaller number of appendages per chasmothecium. The appendages are much longer, 1.5–4 times as long as the chasmothecial diam. (up to 441 µm). Most of the appendages are simple with undifferentiated apices, but the tips of some appendages become circinate. In this respect, *E. pachypodii* can be considered one of the *Erysiphe* species intermediate between the Sections *Erysiphe* and *Uncinula* (Lév.) U. Braun & Shishkoff. Circinate tips of the appendages have not been observed in *E. asclepiadis*. The anamorph of *E. pachypodii* is quite distinct from the conidial state of *E. asclepiadis* by its much narrower, cylindrical conidia, 29.28–41.94 × 8.76–13.56 µm, length/width ratio 2.33–4.3 (according to the original description). Furthermore, *E. asclepiadis* is characterized by a pattern of conidial germination that is characterized by the formation of germ tubes with distinct septa.

2. *Erysiphe robiniicola* and other species of *Erysiphe* s. lat. on *Robinia* spp.

Tai (1946) introduced the name *Microsphaera robiniae* based on a Chinese collection on *Robinia pseudoacacia*. Braun (1987) re-examined type material of this species and published a comprehensive description and illustration. Based on the new generic taxonomy of the *Erysiphales* supported by molecular sequence analyses, Braun & Takamatsu (2000) assigned *Microsphaera robiniae* to *Erysiphe* emend. U. Braun & S. Takam. (incl. *Microsphaera* Lév.) under the new name, *Erysiphe robiniicola,* since the epithet '*robiniae*' was already occupied in *Erysiphe*. Tai's species on *Robinia* is characterized by having numerous mycelioid appendages, at first simple, but later irregularly branched. In the monograph of the Chinese *Erysiphales*, Chen et al. (1987) confused *M. robiniae*, known only from the type collection, with *M. subtrichotoma*, another rather common Chinese powdery mildew on *Robinia* characterized by straight, setiform, terminally regularly branched appendages. This was probably based on the assumption that the type material of this species represented an

abnormal collection. This powdery mildew species was described by Braun (1985) and later reallocated to *Erysiphe* (Braun & Takamatsu 2000). Braun (1987) emphasized the close morphological affinity of this species with *Erysiphe palczewskii* (≡ *Microsphaera palczewskii*). Heluta (1989) listed a collection of *M. palczewskii* on *Robinia pseudoacacia* from the Ukraine and reduced *M. subtrichotoma* to synonymy with the former species. Shin (2000) followed the taxonomy of Chen et al. (1987) and assigned Korean *E. palczewskii*-like collections on *Robinia* to *M. robiniae*. *Microsphaera indigoferae* H.D. Shin & Y.J. La (≡ *Erysiphe indigoferae* (H.D. Shin & Y.L. La) U. Braun & S. Takam.) was introduced for morphologically similar collections on *Indigofera* spp. (Shin 1988), whereas Chen et al. (1987) included Chinese material on *Indigofera* in *M. robiniae*. A new Chinese collection of *E. robiniicola* on the new host *Robinia hispida*, which represents the second collection of this species, agrees well with the type material except for somewhat shorter, less frequently branched appendages and a smaller number of 3–5(–6)-spored asci. However, unbranched appendages are also not uncommon in the type material of *E. robiniicola*. Furthermore, the new collection allowed an examination of the anamorph of *E. robiniicola*, which up to now has not been known in detail.

Erysiphe robiniicola U. Braun & S. Takam., Schlechtendalia 4: 13, 2000 FIG. 2

≡ *Microsphaera robiniae* F.L. Tai, Bull Torrey Bot. Club 73: 118, 1946, non *Erysiphe robiniae* Grev. 1824.

MATERIAL EXAMINED: CHINA. GANSU, Tiensuei, on *Robinia pseudoacacia* L., 10 Oct. 1943, Siang *197* (HMAS 05523), holotype of *M. robiniae*. CHINA. XINJIANG, Aksu, Taklimakan Desert, on *Robinia hispida* L., 20 Oct. 2006 and 25 Aug. 2008, Biao Xu (HAL 2271 [A, B] F, and Mycological Herbarium of the Tarim University, Xinjiang, China, HMTRM).

DESCRIPTIONS: Braun (1985: 92; 1987: 314).

ILLUSTRATIONS: Tai (1946: 119, Fig. 6), Braun (1985: 91, Fig. 4; 1987: 315, Plate 92).

Description based on material on *Robinia hispida*: MYCELIUM in thin white patches, causing necrotic discolorations; hyphae branched, hyaline, septate, thin-walled, 2–7 µm wide. APPRESSORIA solitary, one or two, occasionally even three per cell, slightly to distinctly lobed, occasionally nipple-shaped, 2–7 µm diam. CONIDIOPHORES arising from superficial hyphae, position between two septa more or less central to somewhat non-central, erect, up to 100 µm long (without conidia), foot-cells straight, cylindrical or occasionally somewhat curved or sinuous, 30–65 × 5–7(–9) µm, followed by 1–3 shorter cells, basal septum occasionally somewhat distant from the supporting hypha, up to 10 µm. CONIDIA solitary, cylindrical to ellipsoid, (25–)30–40 (–50) × 12–18 µm, length/width ratio 2.0–3.6. CHASMOTHECIA scattered to gregarious, amphigenous, mostly epiphyllous, 85–125 µm diam.; peridial cells irregularly polygonal, 5–25 µm diam. APPENDAGES numerous, equatorial or

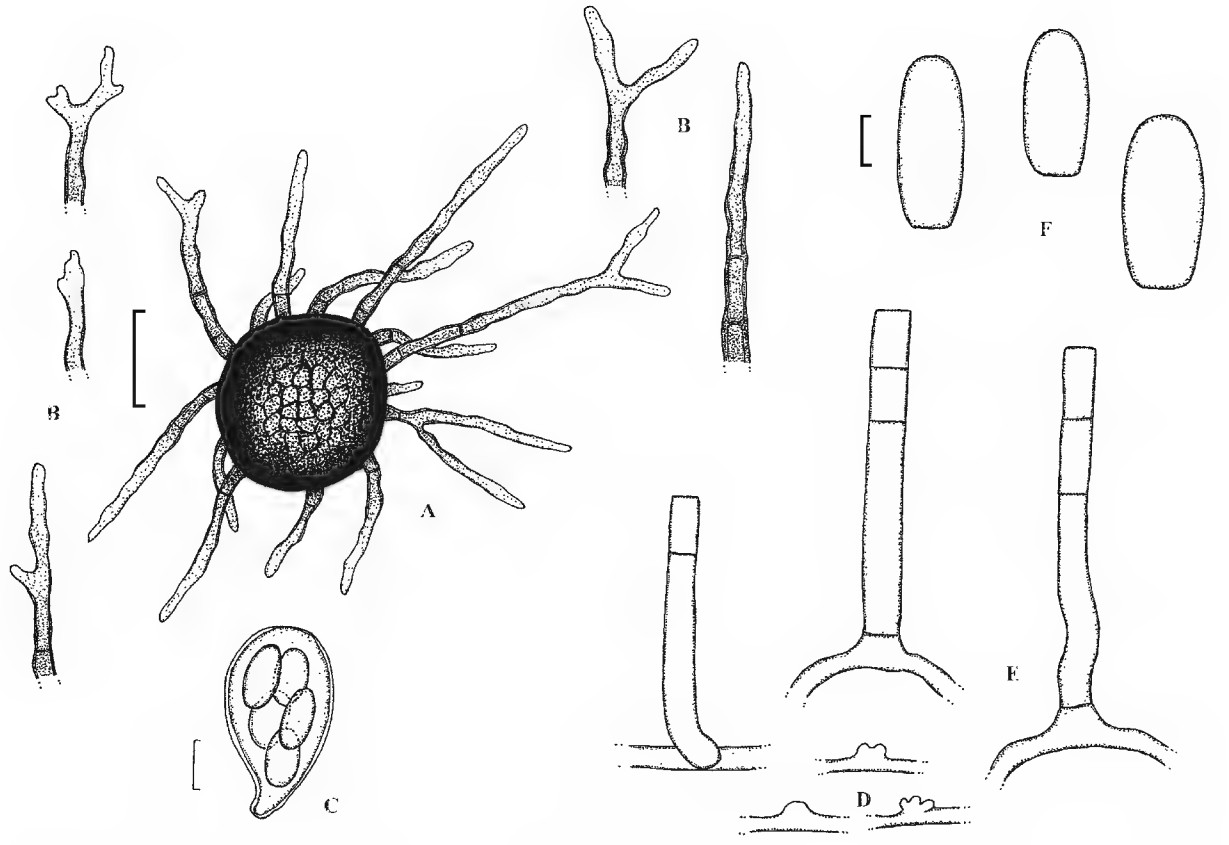

Fig. 2. *Erysiphe robiniicola* (based on HAL 2271 F). **A.** Chasmothecium. **B.** Appendages. **C.** Ascus. **D.** Appressoria. **E.** Conidiophores. **F.** Conidia. Scale bars = 50 µm (A, B), 10 µm (C–F). U. Braun del.

in the lower half, 0.25–2 times as long as the chasmothecial diam., 3–10 µm wide, mycelioid, irregularly shaped, mostly unbranched, but some appendages 1–3 times terminally irregularly branched, rarely branched at the base, short appendages sometimes almost coralloid, 0–3-septate, hyaline, later pigmented below and paler to hyaline towards the apex or brownish throughout, thick-walled below, up to 2 µm, thinner towards the apex, smooth to rough-walled. Asci 4–7, saccate, short-stalked, 40–60 × 25–40 µm, wall up to 3 µm broad, terminal oculus 10–15 µm wide, 3–5(–6)-spored; ascospores 15–22 × 9–14 µm, ellipsoid-ovoid, colorless.

Erysiphe subtrichotoma is unknown in North America although *Robinia* is a North American genus. This raises the question regarding the origin of this powdery mildew fungus. It is more probable that *Robinia* spp. are attacked in Asia by an indigenous Asian powdery mildew species. *E. subtrichotoma* is morphologically indistinguishable from *E. palczewskii*. Schmidt & Scholler (2002) recorded and described the latter species on *Colutea arborescens* from Germany and demonstrated that this fungus was able to expand its host range. Therefore, we follow Heluta's (1989) taxonomic treatment and reduce *E. subtrichotoma* to synonymy with *E. palczewskii*.

Erysiphe palczewskii (Jacz.) U. Braun & S. Takam., Schlechtendalia 4: 12, 2000

≡ *Microsphaera palczewskii* Jacz., Karmannyj opredelitel′ gribov. Tom. II. Muchnisto-rosjannye griby: 339, Leningrad 1927.

= *Microsphaera subtrichotoma* U. Braun, Mycotaxon 22: 90, 1985.

≡ *Erysiphe subtrichotoma* (U. Braun) U. Braun & S. Takam., Schlechtendalia 4: 14, 2000.

HOST RANGE AND DISTRIBUTION: on *Caragana arborescens* Lam. (incl. *C. fruticosa* (Pall.) Besser), *C. boisii* C.K. Schneid., *C. brevispina* Benth., *C. decorticans* Hemsl., *C. densa* Kom., *C. frutex* K. Koch, *C. manshurica* (Kom.) Kom., *C. microphylla* Lam., *C. mollis* (M. Bieb.) Besser, *C. spinosa* (L.) Vahl ex Hornem., *C. ussuriensis* (Regel) Pojark., *Colutea arborescens* L., *Robinia hispida* and *R. pseudoacacia*, Asia (China, Kazakhstan, Korea, Russia, Turkmenistan), introduced in Europe (Austria, Belarus, Czech Republic, Estonia, Finland, Germany, Hungary, Latvia, Lithuania, Norway, Poland, Romania, Russia, Slovakia, Spain, Sweden, Switzerland, the Ukraine) and North America (Alaska, Idaho, Minnesota, North Dakota, Washington) [Braun 1987, Heluta 1998, Scholler 1994, Heluta & Minter 1998, Schmidt & Scholler 2002, Lebeda et al. 2008].

Erysiphe pseudacaciae (P.D. Marchenko) U. Braun & S. Takam. and *Erysiphe robiniae* are additional powdery mildew species of *Erysiphe* emend. (incl. *Microsphaera*) described from *Robinia* species. The latter species belongs, however, to the *Erysiphe trifolii* Grev. complex. Blumer (1933, 1967) and Braun (1987) reduced *E. robiniae* to synonymy with *E. trifolii*. Species of *Erysiphe* s. lat. on *Robinia* can be keyed out as follows:

1 Appendages very long, 2–12 times as long as the chasmothecial diam., often turning towards one direction, flexuous, but not mycelioid 2

1 Appendages shorter, 1–3 times as long as the chasmothecial diam., either stiff, setiform or mycelioid, irregular 3

2 Appendages unbranched or occasionally some appendages 1–2(–3) times loosely dichotomously branched, tips of the ultimate branchlets straight ..... *Erysiphe trifolii*

2* Appendages terminally 1–5 times branched, irregular to rather regular, tips of the ultimate branchlets at least partly recurved when mature ..... *Erysiphe pseudacaciae*

3 Appendages stiff, setiform, continuous or with a single septum at the base, terminally 4–6 times regularly and densely branched, ultimate tips straight ..... *Erysiphe palczewskii*

3* Appendages flexuous, mycelioid, 0–3-septate, unbranched to 1–5 times irregularly branched ..... *Erysiphe robiniicola*

3. *Capnodium lygodesmiae* and *Spolverinia caulicola*

The first reassessment of the "sooty mould" *Capnodium lygodesmiae* dates back to Theissen (1917), who introduced the combination, *Erysiphe lygodesmiae*, based on abundant chasmothecia of a powdery mildew fungus in authentic collections of this species. Ciferri & Batista (1956) examined syntype material of

C. lygodesmiae (Ellis & Everhart, North American Fungi 3216) deposited at BPI and emphasized that they were unable to find any capnodiaceous fungus. They supposed that *C. lygodesmiae* was based on an imperfect sooty mold fungus. However, they found in the type material a "sphaeriaceous fungus" that they described as *Spolverinia caulicola*. In order to clarify the confused taxonomy and nomenclature surrounding *C. lygodesmiae*, type material of this species deposited at NY has been re-examined and the results have been compared with the original data given in the protologue.

Type material of *Capnodium lygodesmiae* contains abundant chasmothecia and superficial mycelium of a powdery mildew fungus strongly infected by the hyperparasite, *Ampelomyces quisqualis*. A collection at NY (ex herb. Ellis, with a handwritten label) was annotated as the holotype, but it should rather be considered a syntype among numerous other duplicates deposited at BPI, NY and various other herbaria that include collections distributed as Ellis & Everhart, North American Fungi 3216 and Fungi Columbiani 616. Therefore, the collection from NY is proposed here to serve as lectotype of *C. lygodesmiae*. This specimen is characterized by having few chasmothecia, but it has abundant mycelium strongly infected by *A. quisqualis*. The white mycelial patches at stems of the host plant turned brownish due to severe infections by this hyperparasite. The original description of *C. lygodesmiae* obviously refers to the hyperparasite: "Perithecia numerous, globose, ovate, or oblong-elliptical, 20–90 × 20–40 µm, ... Sporules not abundant, oblong-elliptical, 5–8 × 3 µm, hyaline." Therefore, the name *C. lygodesmiae* is confined to the *A. quisqualis* element of the type material in accordance with ICBN Art. 9.12:

Ampelomyces quisqualis Ces., Bot. Zeitung (Berlin) 10: 301, 1852.

= *Capnodium lygodesmiae* Ellis & Everh., Proc. Acad. Nat. Sci. Philadelphia 47: 414, 1895, **syn. nov.**

≡ *Limacinia lygodesmiae* (Ellis & Everh.) Sacc. & P. Syd., in Saccardo, Syll. fung. 14: 476, 1899.

≡ *Erysiphe lygodesmiae* (Ellis & Everh.) Theiss., Ann. Mycol. 15: 277, 1917.

Material examined: USA. Colorado, Fort Collins, on living leaves of *Lygodesmia juncea* (Pursh) D. Don ex Hook. (*Asteraceae*), 10 Oct. 1894, C.F. Baker 293 (NY), lectotype of *C. lygodesmiae* designated here.

Theissen (1917) confused *A. quisqualis*, which was the base for the description of *C. lygodesmiae*, with its host, a powdery mildew belonging in the *Golovinomyces cichoracearum* (DC.) Heluta complex, and he introduced the combination, *Erysiphe lygodesmiae*. Ciferri & Batista (1956) examined syntype material of *C. lygodesmiae* from BPI, but they did not confuse this "sooty mould" with the ascomata found at the stems of *Lygodesmia juncea*. Since they did not realize that the ascomycete involved pertained to the powdery mildews (*Erysiphales*), they assigned it to the little-known, doubtful genus *Spolverinia* A. Massal.

(Massalongo 1855–56) and provided a full description and illustration under the name, *S. caulicola* (as '*caulicolum*'). Junell (1964) examined type material of *Spolverinia punctum* A. Massal., the type species of the genus, and demonstrated that this species was based on ascomata of *Phyllactinia* sp. (powdery mildew fungi) blown on the thallus of a lichen. The host of *C. lygodesmiae* is, however, a species of the powdery mildew genus *Golovinomyces* (U. Braun) Heluta that is characterized by having nipple-shaped appressoria, conidia formed in chains and chasmothecia with two-spored asci. Braun (1987) used the misapplied name *Erysiphe lygodesmiae* and reduced it to synonymy with *Erysiphe cichoracearum* DC., now *Golovinomyces cichoracearum*. However, the *Lygodesmia* powdery mildew is morphologically sufficiently distinct from *G. cichoracearum* — by its small (only 18–28 × 12–15 µm) conidia, chasmothecia with very short, often rudimentary appendages, and 2–3-spored asci — that it should be considered a separate species:

Golovinomyces caulicola (Cif. & Bat.) U. Braun, **comb. nov.** FIG. 3

MycoBank MB 512508

≡ *Spolverinia caulicola* ('*caulicolum*') Cif. & Bat., An. Soc. Biol. Pernambuco 14(1–2): 62, 1956.

= *Erysiphe lygodesmiae* auct.

= *Erysiphe cichoracearum* auct. p.p.

HOLOTYPE: USA. COLORADO, Fort Collins, on living leaves of *Lygodesmia juncea* (*Asteraceae*), Oct. 1894, C.F. Baker, Ellis & Everh., North American Fungi 3216 (BPI 600002), holotype of *S. caulicola*.

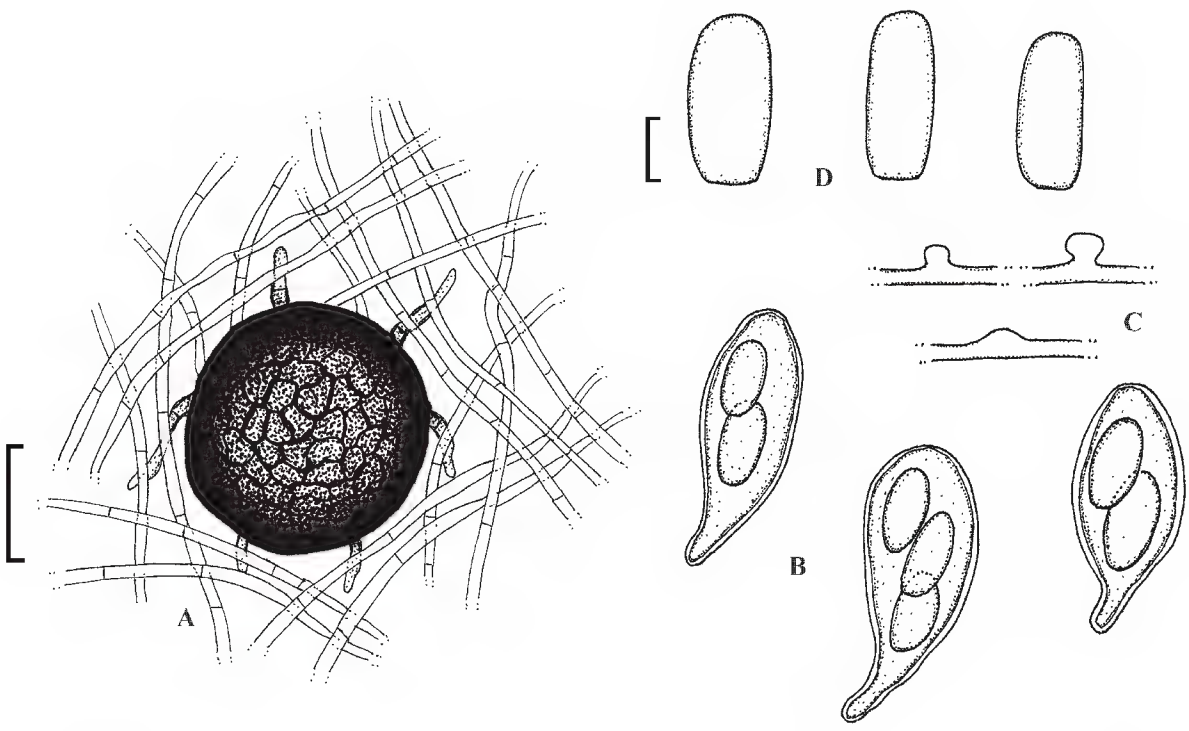

FIG. 3. *Golovinomyces caulicola* (based on type material). **A**. Chasmothecium. **B**. Asci. **C**. Appressoria. **D**. Conidia. Scale bars = 50 µm (A), 10 µm (B–D). U. Braun del.

Material examined: Ellis & Everh., North American Fungi 3216 and Ellis & Everh., Fungi Columbiani 616 (NY 00830153–00830155, 00985691, 00985692), isotypes of *S. caulicola*.

Illustration: Ciferri & Batista (1956: 64, Fig. 1).

Mycelium forming persistent, dense, thick, white patches or covers on stems; hyphae branched, septate, 2–5 µm wide, thin-walled, smooth to rough-walled, white, with age turning yellowish to pale brownish. Appressoria nipple-shaped, 3–6 µm diam. Chasmothecia immersed in the mycelial felt, scattered to gregarious, 70–120 µm diam.; peridial cells irregularly shaped, 10–25(–30) µm diam., walls in front view undulate, thin, 0.5–1.5 µm wide. Appendages few to numerous, shorter than the chasmothecial diameter, sometimes very short and rudimentary, barely distinguishable from the hyphae, mycelioid, unbranched, 3–7 µm wide, septate, thin-walled, smooth, hyaline, later somewhat pigmented. Asci 4–8 per chasmothecium, saccate, short-stalked, wall thin, ca. 1 µm, 2–3-spored, ascospores broadly ellipsoid-ovoid, hyaline, 20–30 × 10–16 µm.

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